

# The Function of Surface Sclerites in Gorgonians (Coelenterata, Octocorallia)

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**Abstract.** Branches of a variety of species of gorgonians representing the common sclerite types were fixed in flexed (bent) positions and examined by scanning electron microscopy. To determine changes in position of sclerites associated with extension and compression, appropriate measures of sclerite density and angle were taken. From these and other data, probable function was hypothesized. Surface sclerites (spicules), called clubs, modify colony flexion by limiting compressibility of the outer cortex when they contact each other. Scaphoids progressively limit extension as their ventral tubercle belts engage similar tubercles on underlying spindles. Radiates limit both extension and compression by catching and locking up after a fixed, free-slide distance. Double-heads severely limit both extension and compression through random orientation of closely packed, spiny protruberences that preclude almost any freedom of movement. Unilaterally spinose spindles act as drawbridge-like, protective covers for polyps. They play no apparent role affecting whole colony mechanics. Possible roles of sclerites as mechanical systems are discussed briefly.

## Introduction

The shapes of gorgonian surface sclerites (spicules) can often be used alone to identify specimens to the generic level. In most gorgonians, surface sclerites differ from those of deeper layers, and these combinations are used for identification to the specific level (Bayer, 1961). Because characteristic sclerite shapes are so highly conserved, we suspect that they are considerably and functionally significant to the organism. If they functioned solely as filler particles to stiffen the coenenchymal gel, the highly specific shapes, sizes, orientations, and positioning of sclerites such as is observed in gorgonians (Verrill, 1868; Kukenthal, 1901; Bayer, 1961) would probably be un-

necessary. They undoubtedly perform this mechanical task (Koehl, 1982; Wainwright *et al.*, 1982; Currey 1984), but stiffening can be done by particles of almost any shape.

The principal support structure of a gorgonian colony is the core or axis composed of gorgonin, which contains a modified collagen (Goldberg, 1976) and which may be mineralized (Lowenstam, 1964; Leversee, 1969). Its stiffness roughly correlates with the broad water movement regimes within which various gorgonian species are found (Jeyasuria and Lewis, 1987; Yoshioka and Yoshioka, 1989). These mechanical properties however, are modified by the sclerite-containing coenenchymal material or cortex (Muzik and Wainwright, 1977; Esford and Lewis, 1990) that surrounds the axis and contains, in a series of cavities, the polyps and gastrovascular canals. In most instances, colonies are dependent on the polyps' ability to efficiently extract nutrients from the surrounding water. Water velocity and direction of movement can change rapidly in response to wave action, so the mechanical properties of the colonies must be specifically tuned to their environment (Koehl, 1982; Vogel, 1988). Polyps feed most effectively at an optimum ambient velocity (Leversee, 1984), and the velocity of food organisms flowing past polyps is kept within this range by the mechanical properties of the axis and coenenchyme (Vogel, 1981).

The coenenchyme is composed of two parts: mesogleal gel and calcareous sclerites. Mesoglea is an example of a compliant composite material composed of a series of discontinuous, randomly oriented, collagen-like fibrils in a hydrated polymer matrix (Chapman, 1953; Gosline, 1971a; Koehl, 1977; Wainwright *et al.*, 1982). Mechanical tests performed on mesoglea from *Metridium senile* reveal its ability to stretch three times its original length under small loads and yet exhibit complete elastic recovery (Gosline, 1971b). The results indicate that this is a time-dependent phenomenon in which quick extension of the material causes greater rigidity than slow extension (Alexander, 1983). This property of the mesoglea must be

considered in addition to the effect of the axial skeleton when considering the mechanical properties of the whole colony. The time-dependent rigidity of the mesoglea translates into resistance by stiffening to high velocity water movement that could flay the colony against the substratum. Compliance occurs at lower velocities, which are less detrimental to colony structural integrity.

Another major determinant of overall mechanical properties of an octocoral colony is the sclerite composition and content of the mesoglea. Sclerites, unlike mesoglea, exhibit little individual flexibility. They are crystalline (Kingsley, 1984) calcium carbonate (Kingsley and Watabe, 1984; Goldberg and Benayahu, 1987a, b; Majoran, 1987; Goldberg, 1988) and are, characteristically of gorgonians, densely packed in the mesoglea. With such characteristic dense packing, the sclerites must interact with any bending or twisting of the colony and consequently affect the mechanics of the whole colony.

In most gorgonians, sclerites are arranged in three distinct layers in the coenenchymal cortex. These layers are usually, though not invariably, distinguishable on the basis of sclerite type (Fig. 1). Immediately surrounding the axis is the axial sheath. Sclerites in this layer are usually short rods, spindles, radiates, or spheroids. These sclerites are densely packed, and are a major component of gastroder-

mal tube walls. Presumably, they function in support of gastrovascular cavity walls and prevent their collapse or kinking during torsion and flexion of the colony (Thibaut, 1983).

The middle cortex adjacent to the axial sheath contains the polyp cavities and branched gastrovascular canals. It is the thickest of all cortical layers. Major sclerite types are spindles, multiradiates, and double heads (Fig. 1), most of which are oriented with their longitudinal axes parallel to the axis of the colony (Bayer *et al.*, 1983). In the genera *Eunicea* and *Plexaura*, middle cortex sclerites can be quite large (up to 1.5 mm).

The outer cortex (the surface layer), usually the thinnest of all layers, is also interspecifically variable in sclerite composition. Generally, only one type of sclerite occurs on the surface of an individual species (Bayer, 1961). The nomenclature concerning the wide variety of sclerite morphs is confusing, but the five broad classes (Bayer *et al.*, 1983) into which surface sclerites of shallow water, Caribbean octocorals can be categorized are: clubs, scaphoids, spindles, radiates, and double heads (Fig. 1). The considerable variation within these basic categories is the basis for much of this confusion. Variants of clubs include sclerites named torches, leaf clubs, balloon clubs, thorn clubs, and wart clubs. Scaphoid variants include

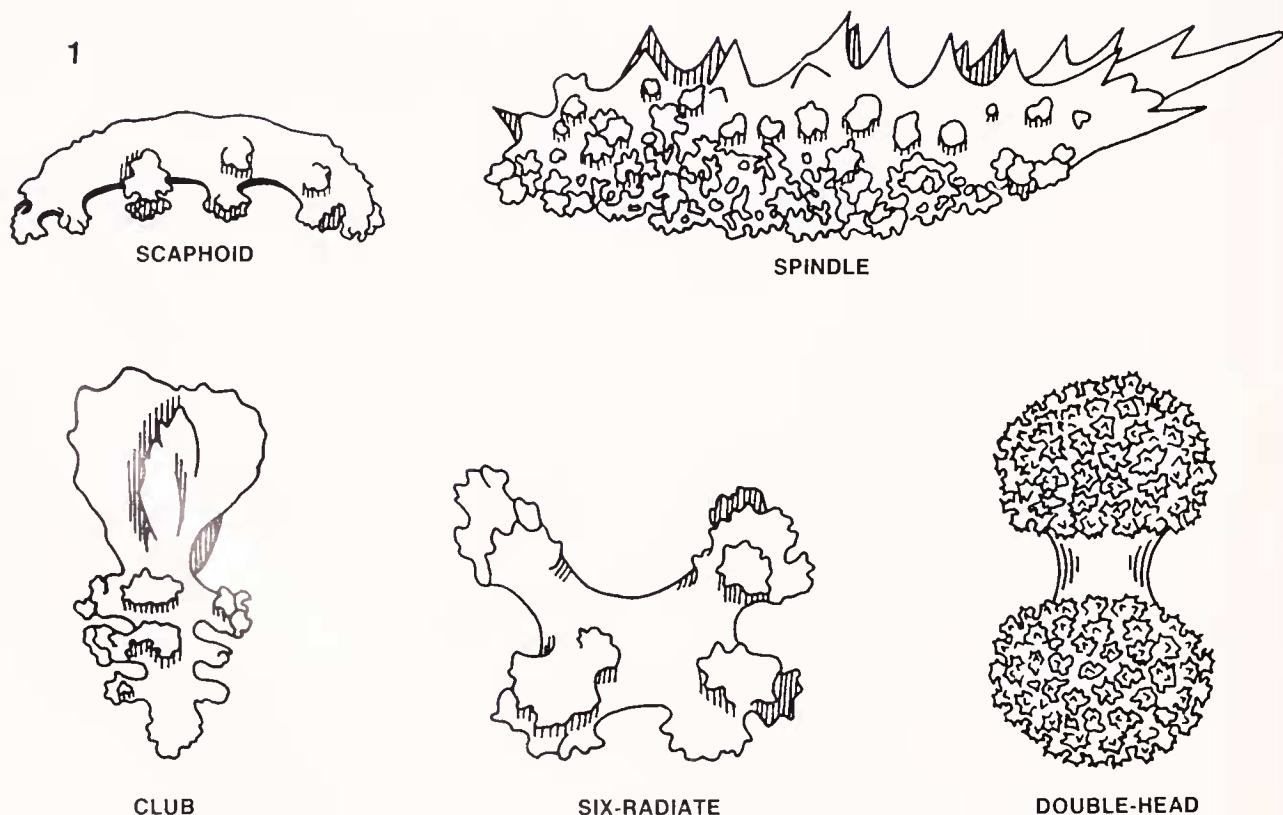


Figure 1. Line drawings of representatives of five of the most common types of outer cortex sclerites that occur in gorgonians. Figures not to scale.

crests, smooth scaphoids (with crests), and scaphoids with transverse crests. Spindle is a general term for any sclerite of fusiform shape, small, medium, or large. Though found on the surfaces of some genera, they are more commonly the principal components of the middle cortex and the axial sheath. One variety of spindle that occurs as an outer cortex sclerite is the unilaterally spinose spindle. Names of radiate variants often correspond to numbers of rays; for instance, six-radiate, seven-radiate, and eight-radiate, but may also be known by such names as antleriform and butterfly. Double heads were formerly known as capstans (Bayer *et al.*, 1983).

Because mesogleal gel is hydrated and contains collagen fibrils (Wainwright *et al.*, 1982), a solid object embedded therein should be capable of motion. Movement under these conditions is described by any of six potential degrees of freedom: pitch, yaw, roll, lateral, vertical, and axial motion (Wainwright *et al.*, 1982; Alexander, 1983). Given this potential, flexion or torsion of the colony as a whole translates into forces that cause the displacement of the sclerites that can be described in terms of degrees of freedom. Limitations on movement are affected by sclerite architecture and orientation (Muzik and Wainwright, 1977).

Drag forces on a basally attached, erect structure will cause bending in the direction of the water flow when the force exceeds the inertial resistance of the material (Vogel, 1981). In general, when a solid bar is bent, it is compressed on the concave surface while being extended under tension on the convex surface. A line marking the midpoint between these two surfaces undergoes no transformation and is therefore named the neutral axis. Tissue on either side of the neutral axis will change in length. Rees (1972), Vogel (1981), and Sebens (1984) have documented a relationship between drag forces caused by waves, tides, and currents and distribution of coral species. Individuals of the same species display variation in growth forms that correlate with the intensity of water movement. Velimirov (1976) noted this phenomenon while studying *Eumicella cavolinii* and additionally noted concurrent sclerite variation. It has been pointed out by numerous investigators that axial mechanical properties are probably modified to varying degrees by the mechanical properties of the coenenchyme and that a major component of the coenenchyme responsible for this must be the sclerites. Scanning electron micrographs of gorgonian cortical layers (Thibaudeau, 1983) hint at complicated relationships between the sclerites in each layer. Somewhat surprisingly, no systematic investigations of the relationship of various different sclerite types with possible mechanical properties of colonies has been published. This examination of sclerite orientation on flexed branches of gorgonians is a preliminary attempt to relate shape to function, and, ultimately, to mechanical properties.

## Materials and Methods

Specimens were obtained from the shallow (0–50 m) coastal waters of Tobago and Cay Sal Bank, Bahamas during field expeditions. Single colonies of *Ellisella barbadensis*, *E. elongata*, *Eumicea clavigera*, *E. calyculata*, *Muricea atlantica*, *M. elongata*, and *Lophogorgia punicea* were collected in Tobago. *Gorgonia ventalina*, *Pseudopterogorgia rigida*, *P. acerosa*, *Plexaurella grisea*, *Eumicea asperula*, *E. laciniata*, *E. knighti*, *Plexaura flexuosa*, *P. homomalla*, and *Pterogorgia anceps* were collected in the Bahamas. Several branches from each specimen were tied in a flexed (bent) position prior to fixation. Angles of flexion could not be kept consistent either inter- or intraspecifically because of large differences in stiffness, flexibility, and thickness between branches. Specimens from Tobago were dipped in 10% formalin, air dried, and transported to Brock University prior to preparation for scanning electron microscopy (SEM). Specimens from the Bahamas were fixed in 3% glutaraldehyde, transported in fixative, then air dried prior to preparation for SEM.

Fresh specimens were collected and examined in the field using a dissecting microscope. Surface sclerites, embedded in mesoglea and coated with mucus, were obscured to the extent that no meaningful analysis of sclerite orientation could be undertaken in the field. Fixation did not alleviate the problem. Only in the *Muricea* could surface sclerites be relatively clearly distinguished.

For SEM, cross and longitudinal sections were cut from various positions on each colony and dipped in sodium hypochlorite solution (Javex, T. M. Bristol Myers) to remove mesogleal gel from embedded sclerites. The time required to remove mesoglea without loosening sclerites varied from specimen to specimen, however, most required 10–40 s. Samples were immediately rinsed in distilled water and dried. Dried samples were mounted on aluminum specimen mounts with double-sided adhesive tape and coated with a thin layer of gold under vacuum in a Polaron PS-3 Sputter Coater. Specimens were examined with a Hitachi model S-570 scanning electron microscope.

We examined 17 species in 8 genera. Because a single analytical procedure could not be applied to all species, a number of measurements were used including sclerite density, space between sclerites, angles of sclerites with axes in the same plane as the colony axis, and angles of sclerites with axes tangential to the colony axis. Sclerite type determined the specific measurement technique used. In all cases, measurements were taken from compressed, neutral, and extended surfaces.

On specimens with surface clubs and double heads, sclerite density was determined. Density was measured directly from the Video Display Terminal (VDT) of the SEM by counting numbers of sclerites in the area bounded by the image edges of the VDT (6.67 mm<sup>2</sup>). An image

scale provided screen area. Sections from each surface (compressed, neutral, and tensed) were measured. Mean and standard deviation values of at least 50 separate locations per surface per sample were determined. To test nonparametrically for intergroup differences, a Kruskal-Wallis one-tailed analysis of variance by ranks was performed (Zar, 1984). The null hypothesis was that there were no differences between the means of the measurements from sclerites on compressed, neutral, and tensed surfaces. If Kruskal-Wallis test results were significant at the 0.05 level of significance or better, the method of multiple comparison (Siegel and Castellan, 1988) was used to determine which differences between medians of the groups were significant.

Because of the interdigitation of processes from adjacent radiates, it was usually not possible to discriminate individual sclerites. Relative density of radiates was obtained by a computer imaging process (MCID Image Analysis System, Imaging Research Inc., Brock University) calibrated to differentiate between areas occupied by sclerites and spaces between them. This was done from SEM photographs with results presented as the percentage of the area of the photographs occupied by sclerites or parts thereof. Data were analyzed using the one-tailed Kruskal-Wallis ANOVA by ranks.

Angles of scaphoids and spindles planar or tangential to the colony axis, respectively, were determined similarly. An acetate sheet, inscribed with a protractor, was affixed to the VDT screen. Using stage controls on the SEM, a sample was rotated to bring the long axis of the colony parallel to the base of the protractor. Compressed, neutral, and extended surfaces were each scanned while maintaining the axis in a constant position relative to the protractor. Measurements of sclerite angles were acquired directly from the VDT screen. Means and standard deviations were determined, again subjecting data to Kruskal-Wallis and multiple-comparison tests.

## Results

Surface sclerites of the seventeen specimens examined were categorized into five main groups: clubs, scaphoids, double heads, radiates, and spindles (Bayer *et al.*, 1983).

### Clubs

A single layer of clubs comprises the outer cortex of all *Eumicea* and *Plexaura* species. All are oriented perpendicular to the colony axis with the rectangular, spiny or rounded plates that form the club's "head" exposed to the surface of the colony while the "handle" projects toward the middle cortex. The bases of the club handles abut middle cortex sclerites, which are usually large, closely grouped spindles oriented parallel to the colony axis. The results of measurements on one colony each of *Plexaura flexuosa*, *P. homomalla*, *Eumicea clavigera*, and

*E. laciniata* are summarized in Table 1a. In all cases, densities were highest on compressed, intermediate on neutral, and lowest on tensed surfaces. Photomicrographs of compressed and extended surfaces appear in Figure 2a. Kruskal-Wallis tests were significant at the 0.05 level but multiple-comparison revealed no significance (Table 1a). When the *Eumicea* species that have much larger clubs than the others, were excluded from the analysis, a significant difference was found between the means of compressed and tensed surfaces. When a branch of a colony bends, clubs on the stretched surface separate; on the compressed surface, they move closer together.

### Scaphoids

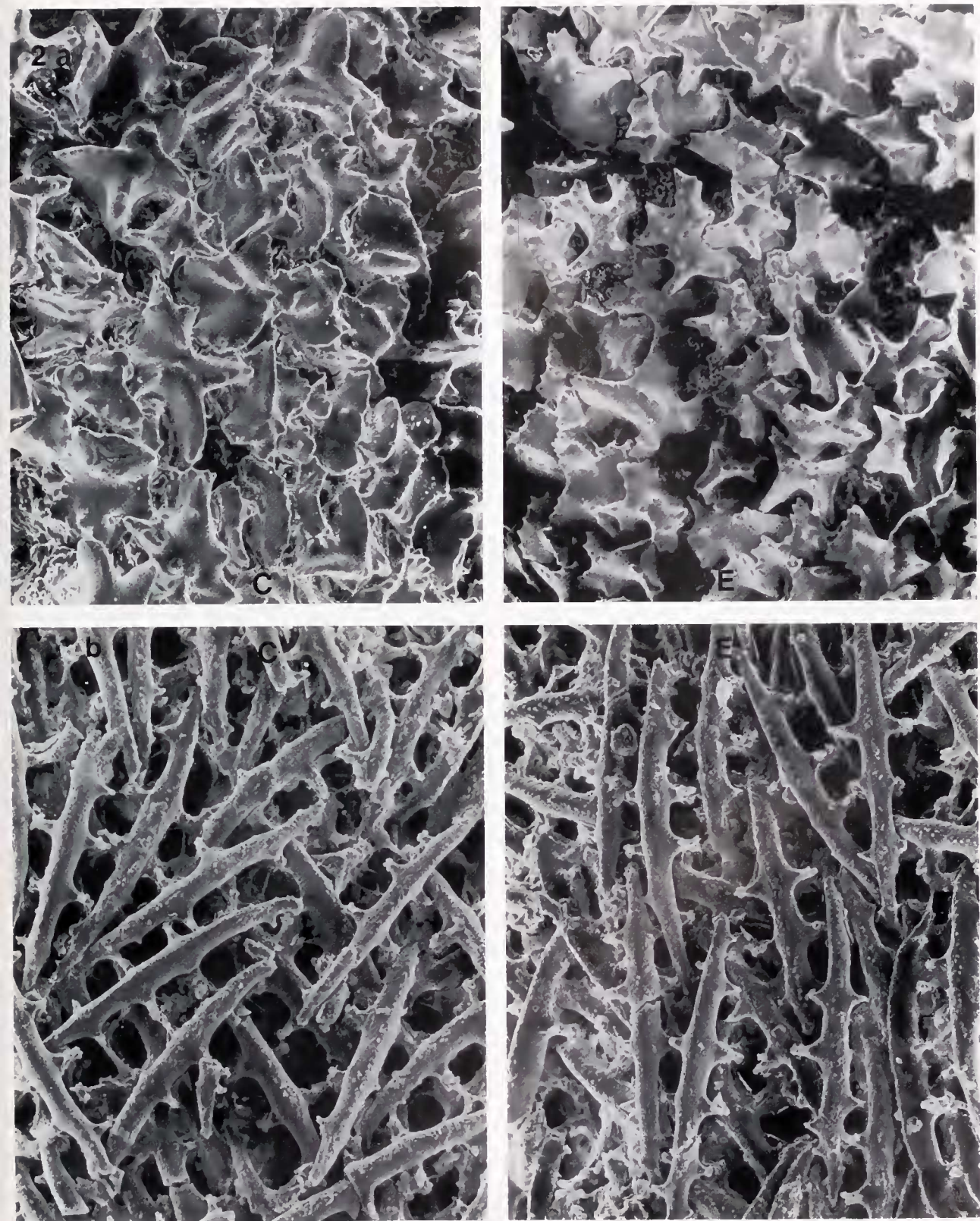
Scaphoids form the surface layer of *Pseudopterogorgia rigida*, *Pterogorgia anceps*, and *Gorgonia ventalina*. They are bent down at the tips and encircled with a series of tubercle belts (Fig. 1). In some genera, the tubercles may be reduced or absent from the convex surface. For these elongate sclerites, orientation with respect to colony axis was determined on the compressed, neutral, and tensed surfaces for the aforementioned species. On the neutral surface of *P. anceps* and *P. rigida*, mean angles of surface scaphoids are  $\pm 30\text{--}36^\circ$  away from parallel with the longitudinal axis. On compression, mean sclerite angles are  $5\text{--}12^\circ$  above those of the neutral surface; on extension,  $6\text{--}14^\circ$  below (Table 1b). Sclerites on the surface of *G. ventalina* are  $28\text{--}36^\circ$  higher than the neutral on compression but only  $9^\circ$  lower on tension. Kruskal-Wallis tests were significant at the 0.01 level (Table 1b), though the multiple-comparison revealed significance only between the means of compressed and tensed surfaces. On stretched surfaces, sclerites rotate into an alignment closer to parallel with the longitudinal axis of the branch. On compression, they rotate into an orientation closer to perpendicular to the longitudinal axis (Fig. 2b).

### Double heads

The double head, or dumb-bell, is characteristic of the genera *Ellisella* and *Lophogorgia*. As the name suggests, these sclerites are simple rods with whorls of tubercles at each end (Fig. 1). They are not organized in distinct layers in the coenenchyme, but appear randomly oriented. No changes in orientation or density can be discerned between compressed, neutral, and tensed surfaces. Kruskal-Wallis test results for intergroup differences between surfaces were not significant (Table 1c). Micrographs of surfaces compression and tension are shown in Figure 3a. Displacement of these small sclerites due to bending of a branch is slight.

### Radiates

The sclerite type found on the surface layer of species of the genus *Plexaurella* is the radiate. In *Plexaurella*



**Figure 2.** (a) Scanning electron micrographs of *Plexaura flexuosa* clubs in surface view under compression (C) where sclerite heads are closely fitted together and under tension (E) where club heads exhibit considerable separation. Mag. 165 $\times$ . (b) Scaphoids of *Pseudopterogorgia acerosa* in surface view under compression (C) and extension (E). Longitudinal axis of the colony is vertical. Note the orientation of most scaphoids under compression at about 40 $^\circ$  from the longitudinal axis, and under extension almost parallel to the longitudinal axis. Mag. 285 $\times$ .

Table 1

Measurements and statistics for surface sclerites on compressed (C), neutral (N), and tensed (T) surfaces of flexed specimens of several species of gorgonians

Species	Flexion angle	C			N			T			P	C-T	C-N	N-T
		(n)	X	S.D.	(n)	X	S.D.	(n)	X	S.D.				
(a) Density of surface clubs per sample area of 6.67 mm <sup>2</sup> . n = number of areas sampled.														
<i>Plexaura homomalla</i>	47°	50	33.4	4.7	51	29.7	2.7	50	24.7	2.7				
<i>P. flexuosa</i> A	12°	54	29.5	1.3	56	26.0	2.0	57	21.4	2.0				
<i>P. flexuosa</i> B	15°	57	31.4	2.7	57	26.7	1.3	56	24.0	2.0	0.05	ns	ns	ns
<i>Eunicea laciniata</i>	35°	59	7.4	0.6	56	4.7	0.6	51	3.4	0.6		(*)	(ns)	(ns)
<i>E. clavigera</i>	13°	61	22.0	2.0	57	19.3	2.0	60	18.0	4.0				
(b) Mean angles of surface scaphoids relative to the longitudinal colony axis.														
<i>Gorgonia ventalina</i> A	37°	150	56	19	159	20	15	138	11	7				
<i>G. ventalina</i> B	37°	167	52	17	191	24	12	181	15	10				
<i>Pterogorgia anceps</i> A	21°	167	44	11	159	36	12	170	22	14	0.01	*	ns	ns
<i>P. anceps</i> B	22°	191	40	11	217	30	9	189	18	12				
<i>Pseudopterogorgia rigida</i> A	39°	143	46	14	121	34	12	131	26	13				
<i>P. rigida</i> B	21°	157	40	9	141	35	10	165	29	10				
(c) Density of surface double heads per 0.33 mm <sup>2</sup> sample area. n = number of areas sampled.														
<i>Lophogorgia punicea</i>	17°	147	24	4	129	22	6	141	26	5	ns			
(d) Mean percentage of sectional area occupied by radiate sclerites.														
<i>Plexaurella grisea</i>	20°	5	87.1	4.3	5	74.6	3.1	5	71.1	2.1	ns			
<i>P. grisea</i>	16°	5	82.4	3.8	5	77.6	2.4	5	75.4	2.1				
(e) Mean angles of evaluation of spindles above the longitudinal colony axis.														
<i>Muricea elongata</i>	30°	413	46	7.5	391	37	6	370	33	3.5	0.10	*	ns	ns
<i>M. atlantica</i>	55°	322	58	11.5	299	39.5	12	319	28.5	11				

Degrees of freedom = 2. P values for Kruskal-Wallis one-way ANOVA. Significance (\*) of multiple comparison tests between ranked medians; ( ) = exclusive of *Eunicea* species.

*grisea*, the six-radiate (Fig. 1) has a main axial rod with three branches on each end, one of which is upturned and longer than the other two, producing an antleriform appearance. The six-radiates are also located in the middle cortex and axial sheath layers; however, they lack the upturned branches and are randomly oriented. Compressed surfaces are comparatively uniform, with few cavities between sclerites, and give an impression of a solid wall of tubercle heads (Fig. 3b"C"). Tensed surfaces are more irregular and indented with more pits, cavities and patches of dark shadow (Fig. 3b"E"). The percentage of area occupied by sclerite as opposed to space was highest on compressed and lowest on extended surfaces (Table 1d). The Kruskal-Wallis test for intergroup differences between surfaces was not significant (Table 1d). These interdigitating sclerites compact on compression, but under tension spaces open up between the interdigitations.

#### Spindles

Large, unilaterally spinose spindles (Fig. 1) of the genus *Muricea* are oriented in tufts of approximately parallel

sclerites (Fig. 4a). In some, but not all species of *Muricea*, these spindles form large, moveable lids for polyp calyces. In those species, which include *M. elongata* and *M. atlantica*, polyps are crowded together so the lids actually cover most of the surface of the colony and form the effective epidermis. One end of each group of 9–17 spindles is butted onto the middle cortex spindles. Butt end and undersurface tuberculation is extremely dense and irregular. The other, spiny end projects from the colony surface and accounts for its prickly texture. These structures form a trough-like, hinged, calycal lid reminiscent of a drawbridge (Fig. 4a). Between the tuft bases, the general surface is covered by smaller, normal spindles and mesoglea. Flexion of the branch results in a change in the angles of the tufts relative to the colony axis with tufts closer to parallel with the surface of the colony on the extended surface and more perpendicular to the surface on compression (Fig. 4a "E" + "C"). Angles of sclerites in tufts are shown in Table 1e for compressed, neutral, and extended surfaces. Kruskal-Wallis tests were significant

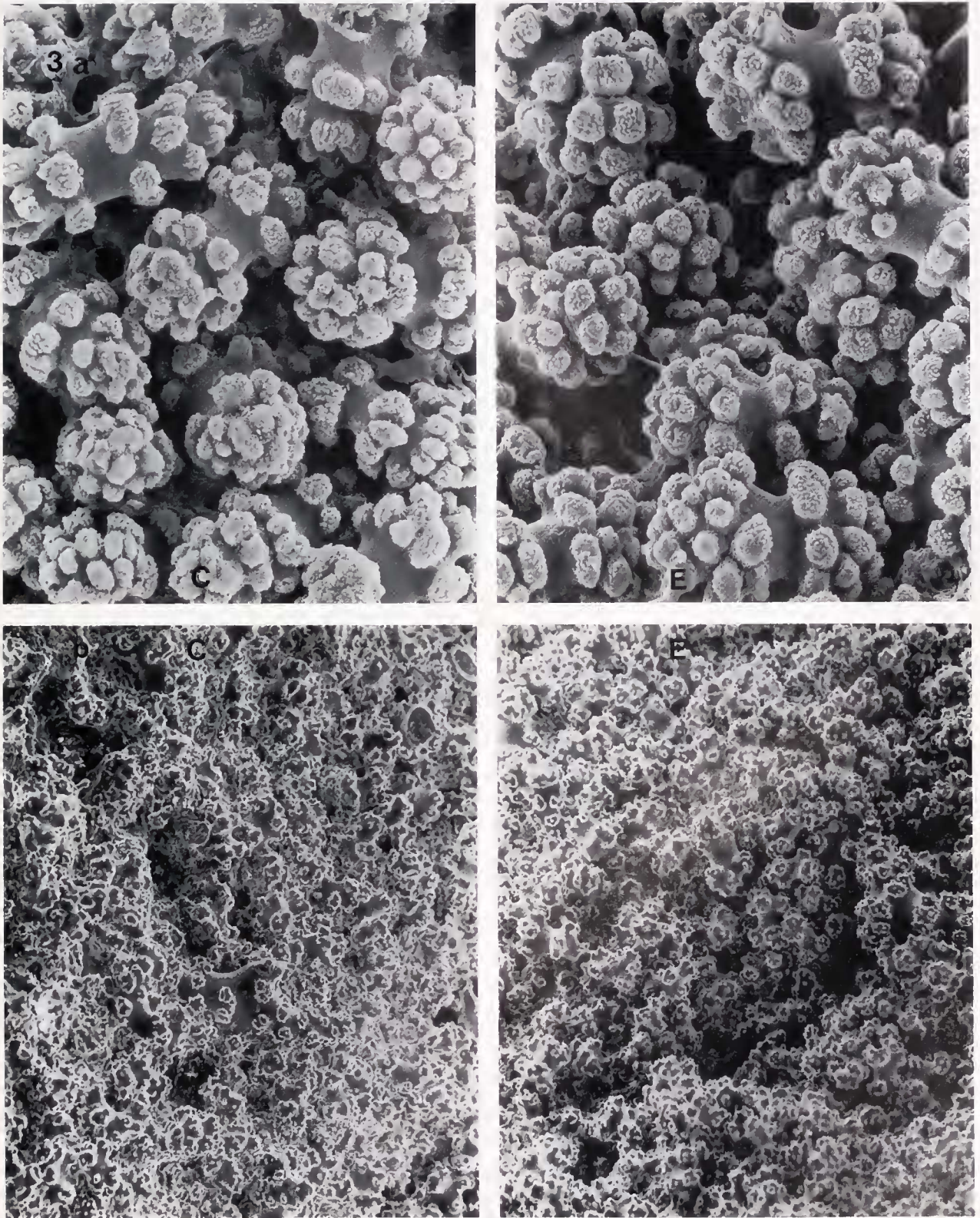
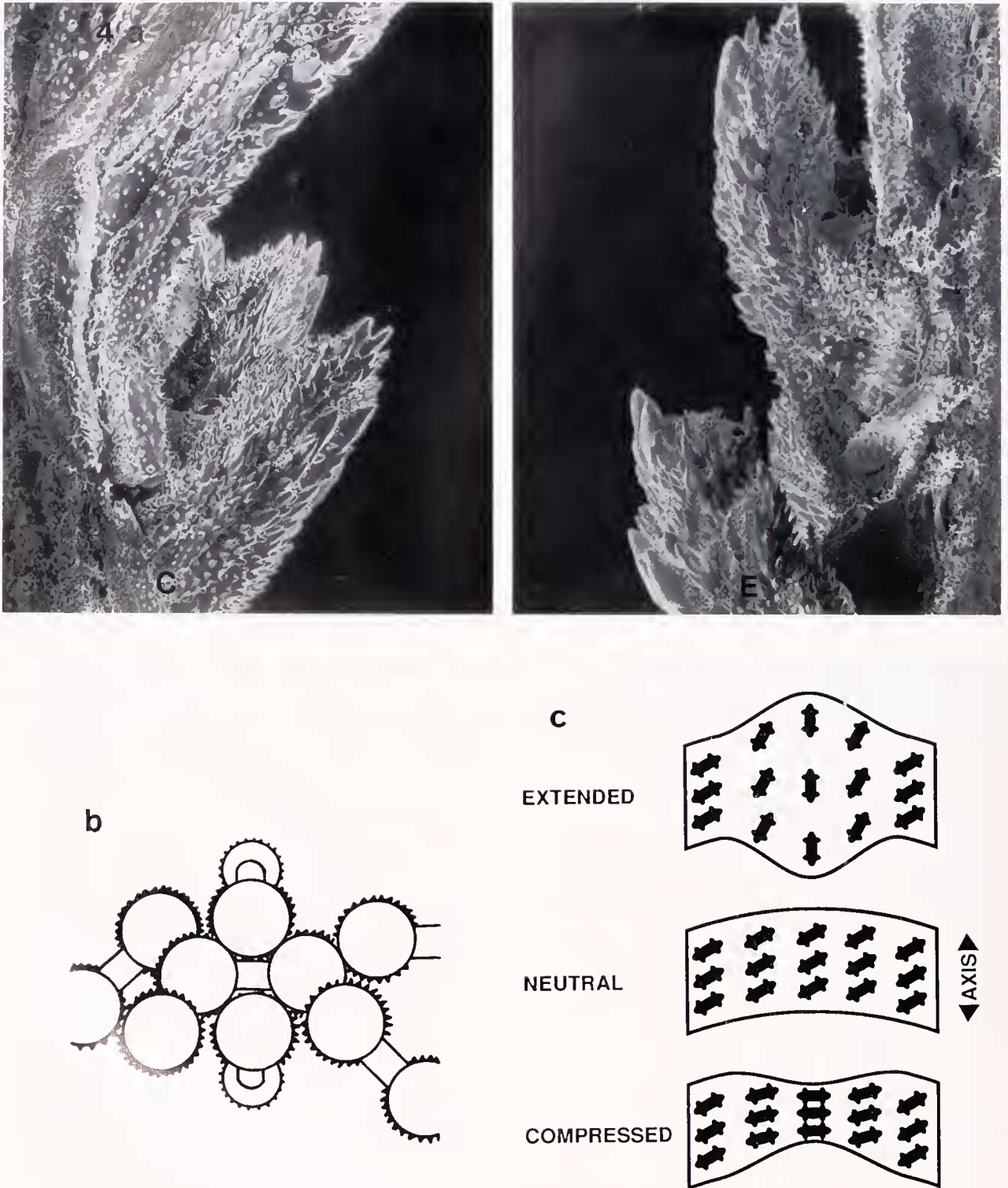


Figure 3. (a) Surface double-heads of *Ellisella barbadensis* under conditions of compression (C) and extension (E). No differences in density or orientation of the sclerites is discernable. Mag. 620 $\times$ . (b) Six-radiate sclerites of *Plexaurella grisea* compressed (C), exhibiting few spaces between sclerites and extended (E), exhibiting more extensive spaces between sclerites. Mag. 105 $\times$ .



**Figure 4.** (a) Unilaterally spinose spindles of *Muricea elongata* under compression (C) and extension (E) to show that under compression, the tufts of spindles are deflected away from the longitudinal axis whereas on extension the spindles assume a position more nearly parallel with the axis of the colony. Longitudinal axis of the colony is vertical. Mag. 35 $\times$ . (b) Diagrammatic representation of possible function of double-heads. Random orientation of spine-covered double-head sclerites tends to preclude any but the slightest motion of sclerites relative to each other. These probably function primarily to increase coenenchymal stiffness. Approx. mag. 500 $\times$ . (c) Diagrammatic representation of translational and rotational movements of



at the 0.10 level, and multiple-comparison revealed a significant difference between the means of compressed and tensed surfaces.

When a plant stem is bent, thorns, bristles, and hairs on the outside of the curve tend to go erect, fan out over the outside of the curve, and project away from the surface. On an intuitive level, this would be expected of the *Muricea*, but the opposite happens. The bristle-like tufts almost lie down on the surface of the outer curvature. On the inside of a bend, spines or bristles fixed at an acute angle to the longitudinal axis tend to assume a more acute angle closer to the inside surface of the curve. Again, the opposite occurs with *Muricea*.

### Discussion

The microscopic size of sclerites and the surrounding mesogleal matrix make it difficult to even visualize the relationships of sclerites to one another. Measurement and characterization of forces acting on individual sclerites when the colony is subjected to stresses of various kinds is truly daunting. Fixation and dehydration undoubtedly alter the properties of the mesoglea and cause some shrinkage of the highly hydrated gel if it is at all similar to other coelenterate mesoglea (Alexander, 1964; Gosline 1971a). The extent of shrinkage has not been measured for these species, but we estimate it to be less than 10%. On the one species we have measured on drying (a *Menella* sp. from the Indian Ocean), shrinkage was about 5% at seven different locations on the specimen. The volume fraction of sclerites in the coenenchyme of gorgonians is high, and it probably varies interspecifically although volume fraction, again, has not been recorded. For the aforementioned *Menella* species from the Maldives, it was 45% in the tips and 55% in primary branches. Because sclerites provide support for the mesoglea (Muzik and Wainwright, 1977; Koehl, 1982; Currey, 1984), their volume is probably responsible for the low shrinkage. We have assumed that all sclerites are relatively uniformly surrounded by mesoglea. In that event, shrinkage should affect all sclerites similarly so their relative positions should remain similar to that *in vivo*.

Removal of surrounding mesoglea with hypochlorite bleach loosens surface sclerites. In most species, examination with the dissecting microscope clearly reveals when the process has gone too far; *i.e.*, the surface layer is absent. If the process has not gone far enough, sclerites or large parts of them remain obscured by mesoglea. Care was

taken to minimize dislocation, but mesoglea removal by hypochlorite is a rather imprecise procedure. The positions of individual sclerites may change during uncovering and subsequent processing and thus alter surface sclerite orientation. The degree of disturbance depends upon the extent to which sclerites loosen and interdigitate with neighboring sclerites.

The following ascribed functional relationships are postulated as those that can be reasonably implied from the rather crude manipulations to which the individual colonies were subjected.

#### *Possible function of clubs (Fig. 5)*

Clubs occur as outer cortex components in four of the *Plexaura* and *Eumicea* species examined. All exhibited a higher density of clubs on compressed surfaces than on either neutral or tensed ones. This illustrates vividly the contention of Wainwright *et al.* (1982) regarding the altered density of material on either side of the neutral axis of a bent bar. Compression on a colony surface causes the clubs to move laterally until they contact adjacent clubs. Resistance to compression increases substantially at this point.

Compression or tension of the colony surfaces would also cause a similar compression or tension of the mesogleal gel that surrounds each embedded sclerite. The mesoglea, an elastomer, responds to such forces like a rubber ball being compressed or stretched. Lateral compression of the ball causes its vertical diameter to increase, whereas stretching reduces this diameter (Wainwright, 1988). Clubs, held in the gel by the handle tubercles, move in a direction perpendicular to the colony axis and also separate from each other on extension. Immediately subjacent to the outer cortex is a layer of large, thick spindles in close contact with each other. On the surface under tension, the mesogleal gel stretches over the convex surface and pulls the surface clubs toward the middle cortex spindles. As the tubercles at the base of the club handles come in contact with the irregular tubercles covering the spindle surface, they catch. The first clubs to become engaged are those whose handles are nearest the spindle tubercles. As the clubs are carried along, they contact the clubs that have engaged spindle tubercles. This causes them to bunch up, leaving a series of cracks or spaces.

Compression of the colony surface compresses the mesoglea, which translates into a vertical force acting un-

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elongate bodies (sclerites) embedded in an elastomer on one half of the surface of a cylinder. Conditions of compression, extension, and no stress (neutral) are illustrated. Inclusions (sclerites) are oriented at about 50° with respect to the longitudinal axis under all conditions of no stress. Maximal displacement occurs in the mid line of the bending plane of the cylinder. Intermediate displacement extends laterally each way from the center of the plane of bending, one quarter of the distance around the circumference, where no translation or rotation occurs.

derneath the surface clubs that lifts them off the spindle surface and disengages them (Wainwright, 1988).

Clubs can move in all six of the degrees of freedom of movement (Alexander, 1983). Pitch, yaw, lateral, and vertical movements of the clubs are all in the plane of the surface layer. Axial motion occurs during compression and tensing of the gel, which increases and decreases the distance between the base of the clubs and the middle cortex spindles. Roll, pitch, yaw, and lateral movement of the clubs are limited by the proximity of adjacent clubs and the degree to which they interdigitate with the plate tubercles on the heads of adjacent clubs. Colony torsion as a whole results in some degree of club rotation. Interdigitation of tubercles enables the rotational forces on a sclerite to be passed to adjacent sclerites.

#### *Possible function of scaphoids (Fig. 5)*

In unbent specimens, elongate scaphoids form a surface layer with all sclerites oriented in parallel, as in *G. ventalina*, or with sclerites in two parallel orientations as in *P. anceps* and *P. rigida*. Scaphoids are oriented at approximately 30° away from the longitudinal axis of the colony. Because the sclerites are in a sheet-like layer on the outside of a cylinder, the forces of tension and compression are applied asymmetrically to the sheet when the cylinder is bent (Koehl, 1982). The greatest displacement or distortion occurs in the center of the plane of flexion, with lesser displacement occurring out and around the sides of the cylinder toward neutral axes. On tension, translation will be toward the extremities of the longitudinal axis; rotation of the elongate sclerites will be toward the center of the plane of flexion, which is toward the longitudinal axis (Fig. 4c). Compression reverses both movements (Koehl, 1982).

Surface sclerites do not function completely independently of subjacent middle cortex sclerites. In the species examined, these are belted spindles oriented close to parallel with the longitudinal axis. We think the surface sclerites interact with middle cortex sclerites and modify the mechanical properties of the axial skeleton (Muzik and Wainwright, 1977). When a cylinder is bent, the outside undergoes further displacement than the inside (Wainwright, 1988). Therefore, sclerites on the outside will move more than those of inner layers. On a tensed surface, the mesogleal sheet containing the surface sclerites becomes thinner on being stretched (Wainwright, 1988) and pulls its sclerites down into contact with the middle cortex spindles. These spindles are nearer the center of the cylinder and will not be displaced toward the center as much as surface sclerites. It is unlikely that they will undergo as much translation or rotation even assuming complete freedom of movement. Consequently, the ventral tubercles of surface scaphoids will engage with dorsal tubercles on the underlying spindles and both their translational

and rotational movement will be limited. The response will be graduated. As more tubercles engage, resistance to stretch will increase.

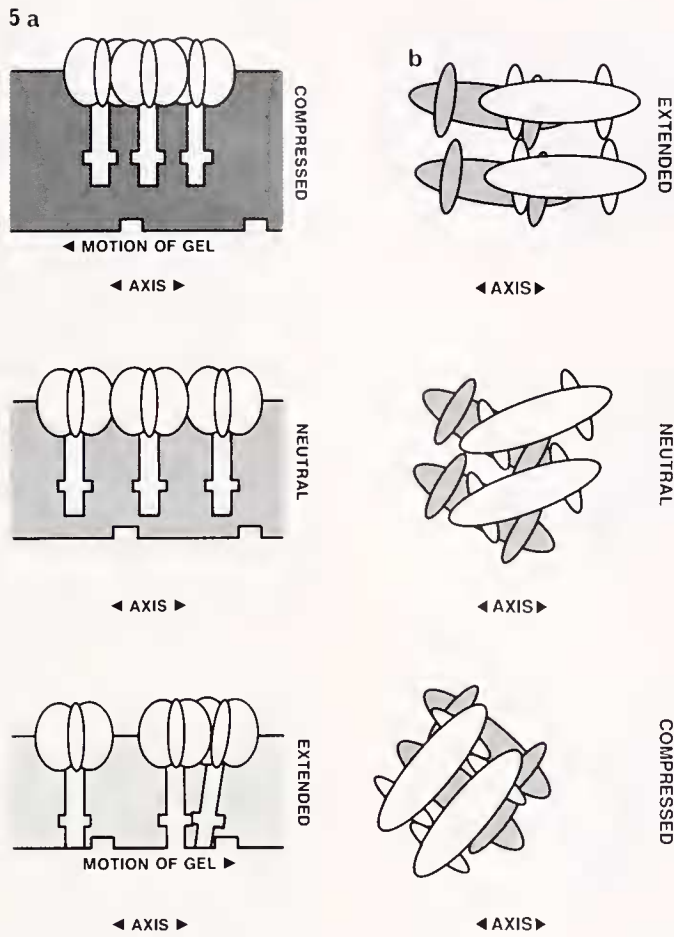
Compression thickens mesogleal gel and lifts scaphoids off the backs of underlying spindles. With tubercles disengaged, sclerites are free to undergo translation and rotation in directions opposite those of extension.

#### *Possible function of double heads (Fig. 4)*

No change in density of double heads was quantifiable on either compressed, neutral, or tensed colony surfaces. This could be an indication that either there is no difference between the three surfaces, or the techniques used were not sensitive enough to elucidate any differences. Close examination of double head terminal tubercles reveals a series of closely grouped tubercles covered with fine spines, almost like a Velcro ball surrounding each terminus of the central rod. The tuberculation suggests that any motion involving sliding of one tubercle over one of an adjacent sclerite would be inhibited by a high frictional force. The fine spines would limit freedom of motion of surface sclerites in pitch, yaw, lateral, vertical, and axial motion but would not completely inhibit roll. However, random sclerite orientation negates any overall effect that sclerite roll may have on colony flexibility. The main function of this type of sclerite, and its random orientation, is probably to increase coenenchyme stiffness. Because there is some mesoglea between sclerites, there is some slight freedom for movement of sclerites relative to each other that produces limited flexibility. Due to the small size of the sclerites (0.075 mm in length), even a small amount of movement could translate into considerable flexibility over a relatively short distance of a few centimeters.

#### *Possible function of radiates (Fig. 5)*

Six-radiate sclerites of the species *Plexaurella grisea* are found in both outer and middle cortex layers, but those in the middle cortex lack the extended rays of those on the surface. The orientation of the surface sclerites is irregular, and the long processes characteristic of them are deeply embedded in mesoglea. Individual sclerites could not be discriminated for counting, but results indicate a smaller sclerite area on sections under tension than under compression. Six-radiate sclerites have a series of smooth surfaces that terminate in large tubercles. The tubercles resemble cauliflower heads designed to catch on anything moving past them from any direction. When the smooth surfaces of two adjacent sclerites or their interlocked arms are in contact, they can slide across each other until the tubercles catch. Because the arms of these sclerites interdigitate, both compression and extension (and torsion for that matter) are limited by the same mechanism. By analogy, the model of a chain can be used to explain the mo-



**Figure 5.** (a) Diagrammatic representation of possible function of clubs from a lateral perspective. On compression of the coenenchyme, clubs are lifted by the compressed gel and moved into tighter contact and interdigitation with each other thereby increasing resistance to compression. On the neutral surface, club head processes interdigitate but are not in contact; their handles are not in contact with underlying spindles. On extension, clubs are pulled by elastic coenenchymal gel into contact with surfaces of large underlying spindles and spread apart. Some club handles catch tilt and jam on tubercles of underlying spindles. Approx. mag. 500 $\times$ . (b) Diagrammatic representation of possible function of saphoids from a surface perspective. In a neutral state of compression, surface saphoids are oriented at an angle of about 30 $^{\circ}$  to underlying, tubercle-belted spindles. On extension, surface saphoids are pulled by stretching coenenchymal gel down onto subsurface spindles. Because surface sclerites undergo greater translation (longitudinal movement) than underlying spindles, when their tubercles engage those on the backs of the spindles, they are rotated toward the longitudinal axis. On compression, surface saphoids are lifted off the backs of spindles and disengage. They are free for both translation and rotation due to mesogleal compression. Because of their orientation in the neutral state, rotation is toward perpendicular *vis a vis* the longitudinal axis. Approx. mag. 200 $\times$ . (c) Diagrammatic representation of possible function of radiates. In neutral compression, radiates with spiny tubercles on the ends of smooth arms are loosely interdigitated. Upon compression, tuberculated arms slide over the smooth portions of the interdigitations until tubercles contact nearby tuberculated heads. On extension, the same process occurs in reverse. This mechanism defines the limits of both extension and compression. Approx. mag. 200 $\times$ . (d) Diagrammatic representation of possible function of unilaterally spinose spindles. Spindles form a pivotable cover attached to one side of the polyp. On compression, underlying cortical spindles and coenenchymal gel squeeze gastrovascular canals and force fluid into the polyp, which expands and forces the overlying lid of unilaterally spinose spindles to pivot and extend out from the longitudinal axis of the colony. Extension, which moves the cortical spindles in the opposite direction, pulls fluid from the polyp into the gastrovascular canals, deflating the polyp and pivoting the lid in toward the colony axis. Approx. mag. 50 $\times$ .

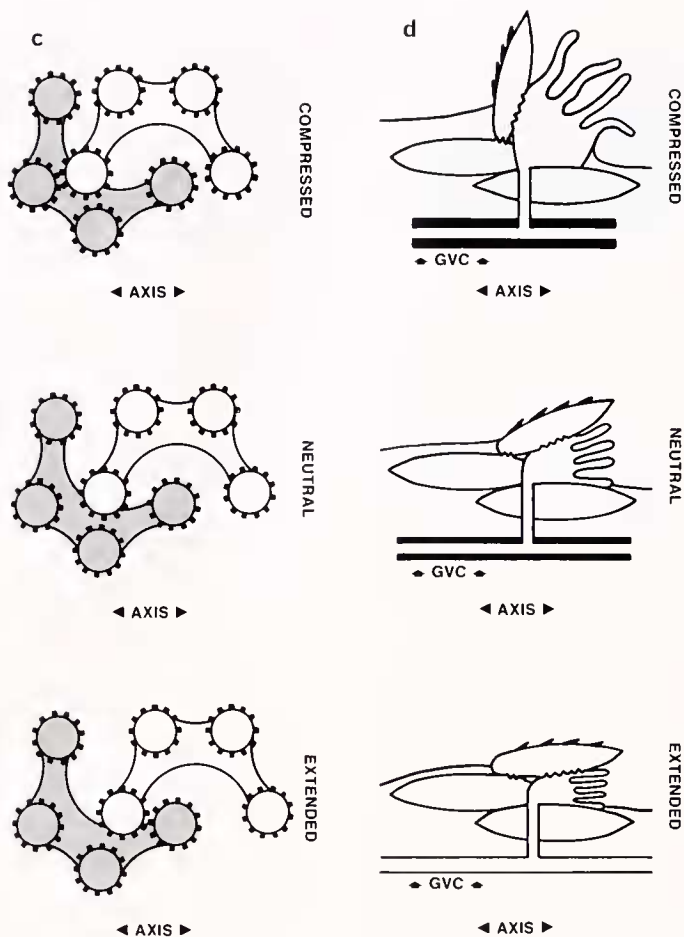


Figure 5. (Continued)

tion of a series of interacting six-radiates. Chain links have an extended smooth surface (smooth portion of the arms) on which interlocking links can slide, but which are terminated abruptly by the terminal cross piece (tubercles). Compression of the colony surface causes the smooth rays to slide along each other until the tubercles come into contact. When all radiates are compressed to the extent that they can no longer slide with respect to each other, the surface becomes rigid. Extension pulls the radiates apart along the smooth ray axes until terminal tubercles come in contact with the adjacent sclerite tubercles. This limits further extension of the coenenchyme.

#### Possible function of unilaterally spinose spindles (Fig. 5)

Compression or extension results in a change in angle of tufts relative to the colony axis with tufts closer to parallel with the colony on extension and more perpendicular to the colony on compression. A possible explanation for these results involves the interaction of the middle cortex spindles, mesogleal gel, and the gastrovascular system of the colony. The feeding polyps are located in the crevice

between the calycal trough and the colony body. In a neutral state, the tufts extend out from the colony surface at an angle of approximately  $40^\circ$ , which allows the polyp tentacles to be extended from the crevice for food capture. Compression of the layer of mesogleal gel is translated into a lateral force that pushes the spindles away from the colony surface. Additionally, compression of the gastrodermal tubes that link the polyp cavities increases the internal pressure and forces water out into the only possible exit—the polyp cavities. Because the gastrodermal tubes are linked directly to the polyp gastrocoel, expulsion of water inflates the polyp bodies. Inflation of the polyps results in a force applied to the ventral surface of the surface tufts, pushing them away from the colony surface. There may be a muscle, tensor system associated with gastrovascular canals and the epidermis (Chapman, 1974) that acts on compression (Chapman, 1970; Esford and Lewis, 1990; and Lewis, unpubl. results). Contraction of myoepithelial cells on the back of the tuft will pull it into a more erect position away from the longitudinal axis of the colony. Contraction of the longitudinal muscles of the gastrovascular canals (Hyman, 1940) will shorten the ca-

nals, increase pressure, inflate the polyp, and push the tuft away from the surface.

On the extended surface, the gel stretches over the convex colony surface and pulls the tuft toward the colony axis. Extension of the surface results in negative or at least lower water pressure in the gastrodermal tube system. This pressure decrease causes the polyps to deflate and draws the tufts closer to the colony surface. Alternately or additionally, relaxation of the myoepithelial and gut muscle systems may permit the passive mesogleal stretch to pull the calycal tufts in toward the colony surface. There could also be a different set of muscles associated with the polyp that retracts the tufts.

### Mechanisms

The foregoing are illustrations of simple and complex interactions of mechanical systems (sets of material objects) termed mechanisms. If a system is underconstrained and has one or more possible modes of motion, it is called a mechanism (Goodman and Warner, 1963); if it is completely constrained against motion, it is called a frame. The mechanism is therefore an assembly of bodies connected in such a way that movement of one causes a required movement of another (Alexander, 1983). The sclerites in gorgonians resemble links as opposed to joints (Alexander, 1983). Links are rigid bodies (Hunt, 1978). They act as passive devices for limiting the freedom of movement of the entire structure. In gorgonians, such passive mechanisms can be used because no muscle or tendon system is required for bending movements of the entire attached colony. The elastic properties of the axial skeleton in conjunction with wave action or current reversal, returns the colony to or through the upright (erect) position. The sclerites limit the extent of these movements.

Clubs form a simple mechanism that acts in one plane to limit compression. In addition, the interdigitation of vertical plates on the heads of clubs enables torsional forces to be transmitted, but this was not investigated.

Surface scaphoids only limit extension when their ventral tuberculations engage the dorsal tubercle belts of underlying sclerites.

At the limits of both extension and compression, six-radiates possibly produce a braced, three-dimensional framework. Though the system is a mechanism, at its limits it may approximate Maxwell's lemma (Parkes, 1965) a theorem for optimization of a space frame with all members in either tension or compression (Wainwright *et al.*, 1982).

The mechanism illustrated by the double heads, which restrict movement in any plane, may be an example that approaches a Michell structure (Wainwright *et al.*, 1982). In these orthogonal, space frameworks, some members are under compression, others under tension.

At their limits, all of these sclerite mechanisms may act as rigid space frames. Between those limits, the sclerite-

collagen-gel system possibly functions as a tensegrity structure or what Vogel (1988) calls an unbraced framework. Verification of these suggestions awaits much more detailed observation and experimentation. This preliminary survey has revealed a hitherto unrecorded, compositionally novel, and complicated skeletal system that probably acts in conjunction with and modifies the more conventional axial support system of gorgonian colonial structures.

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